New Observations of Leaf Movements in *Pinguicula* (Lentibulariaceae)

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Introduction

The authors of the most recently published, significant carnivorous plant monograph concluded that "little attention has been paid to the movement in leaves of *Pinguicula* since it was first described and experimentally studied by Darwin (1875)...." (Juniper *et al.*, 1989, p. 108). Darwin's technique was to place prey on the leaf and observe how the leaf rolled upwards and sometimes enclosed the prey. While many aspects of insect trapping in butterworts have been dealt with (Heslop-Harrison, 1970, 1981; Heslop-Harrison & Knox, 1971; Karlsson *et al.*, 1987; Vasilev & Muravnik, 1986; Zamora, 1995; and others), few authors have discussed leaf movement by either using or repeating Darwin's experiments.

The reason for leaf movement in *Pinguicula*, especially the rolling of the leaf margin, is not well understood. The following opinions have been mentioned in the literature:

1)Leaf margin rolling brings more glands into contact with the prey, analogous to the case with *Drosera* (Darwin, 1875).

2)The involute leaf margins help to hold the secretions in place (Lloyd, 1942).

3)Movement brings about a faster digestion; the inflection of the margin over an insect exposes a far greater area of its body to direct contact with the glands. Additionally, the inflection covers and thus protects the prey item from rain (Slack, 1988).

4)The curling movement makes it difficult for kleptoparasitic ants to detect and extract the prey (Zamora, 1990).

None of these authors conclusively defined the principal function of leaf movement in *Pinguicula*. We searched for the answer using a modified version of Darwin's method.

Material and Methods

Leaf movements were documented in *Pinguicula bohemica* Kraj. and *P. grandiflora* Lam. cultivated at the Botanic Garden Liberec. Pieces of meat about 2-4 mm in size were used as the experimental prey and were placed halfway between the leaf margin and the midrib. Pictorial and photographic records of consequent leaf movements were made.

Principal Function of Leaf Movement

Juniper *et al.* (1989) have described carnivorous plants as those that exhibit the "carnivorous syndrome", which they define as having six attributes with respect to prey: 1)Attract, 2)Retain, 3)Trap, 4)Kill, 5)Digest, 6)Absorb useful substances. Since leaf movements in *Pinguicula* play no role in the capabilities 1-4, they must have a

Figure 1: Reaction of *P. grandiflora* to food.


A—at 0 hours, meat is put on a leaf.


B—at 2.5 hours, a capillary tube is formed.


C—at 8 hours, the reaction is maximal, but the piece of food remains outside the tube.


D—at 98 hours, the food has been digested completely and the leaf is rolling back.

function in either digestion or nutrient absorption.

If a large prey item is captured on a butterwort leaf, its consumption is accompanied by movement of a leaf margin in several (but by far not in all) species of the genus. The movement is very slow. Umrath (1944) was the first to measure changes in electric potentials in leaf tissue during these movements. He found it was about 0.1 V for *Pinguicula vulgaris*. These impulses extended a very small distance from a piece of food, and the "action potential" of an excitation impulse was scarcely detectable 6 mm from the spot to which food was applied. Digestion and nutrient absorption might seem to involve only a very small area of a leaf.

In our experiments with *P. grandiflora*, a piece of food was situated a certain distance from the leaf margin (in contrast, Darwin placed prey on either the leaf midrib or margin). The effect of movement was surprising. The leaf-margin rolled lengthwise to form a long tube. The food was not enclosed by this tube, but rather remained just outside it. As such, digestion proceeded without the leaf protecting the prey from other influences. Ultimately the marginal leaf tube lengthened into a very long capillary-like structure, and the area of nutrient absorption was thus maximized (Figure 1).

The response to food by a young *P. bohemica* leaf that was still in a considerably erect position was particularly interesting (see Figure 2). The liquid produced by the leaf, enriched by nutrients from the prey, flowed down the leaf under the influence of gravity. Consequently, parts of the leaf margin far from the piece of food was excited, and in response formed a marginal tube which drew in the liquid by capillary action. The liquid acted as a conductor of excitation in the process, and the marginal tube acted to increase the area of nutrient absorption.

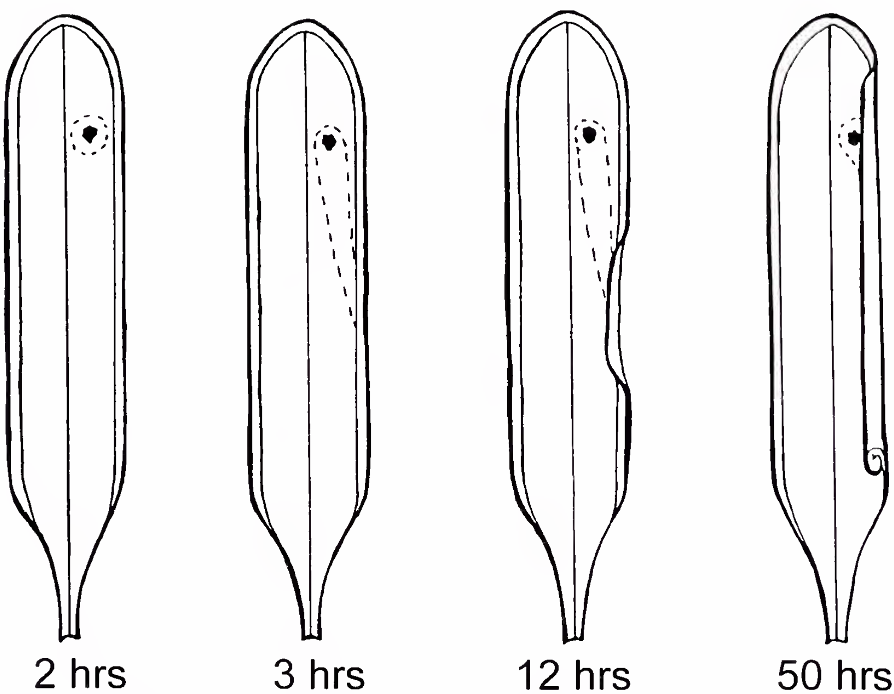

Figure 2: Reaction to food in a young, erect *Pinguicula bohemica* leaf. A—the first secretions are produced. B—the liquid flows towards the lower margin. C—a capillary tube is formed far from the piece of food. D—the tube, aiding the nutrient absorption, is maximally extended while the food is digested alongside it.

Conclusions

It was observed that the slimy liquid product of digestion was dispersed under the influence of gravity. It was also observed that when this liquid flowed into the long tube created by the rolled leaf margin, it was distributed via capillary action over a much larger area of the leaf surface. While Umrath (1944) showed that electrical leaf impulses are responsible for the very local excitation of glands and rolling leaf margin, our observations show that the nutrient-rich liquid itself can be considered a vehicle for long-distance excitation.

From these observations, I can emphasize the sixth attribute of the carnivorous syndrome (absorption of nutrients) as the actual purpose of leaf movements in these species of butterworts. The leaf movement maximizes the absorptive area. While the benefits of leaf movement described in the introduction may be valid, they are not complete without including the effects described in this paper. Butterwort leaf movement aids in nutrient absorption, and not prey digestion.

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Looking Back: CPN 25 years ago

Bill Hanna wrote about an unfortunate perception of *Nepenthes* that he learned about when talking to a botanist from the Singapore Botanic Garden: "In Singapore there are three varieties of *Nepenthes*: *N. ampullaria*, *N. gracilis*, and *N. rafflesiana*. However, it is the official policy of the Ministry of the Environment that they were a potential breeding ground for mosquitos, although she knew of no mosquitos or their larvae in Singapore that were immune to their digestive juices. They enforce this ruling by spraying them thoroughly or physically clearing them completely. But nevertheless, there are still some [persisting *Nepenthes* plants] to be found...."